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A NEW FOSSIL TORTOISE FROM THE THOMAS FARM MIOCENE OF FLORIDA

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No. 11.—*A New Fossil Tortoise From the Thomas Farm Miocene of Florida*

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Several plastra, a nearly complete carapace and additional fragments of a tortoise from the Miocene of Thomas Farm, Gilchrist County, Florida, pertain to an undescribed form apparently ancestral to the giant tortoise of the Florida Pleistocene, *Testudo sellardsi*.

The new species may appropriately be named in honor of Dr. Theodore White whose work on other components of the Thomas Farm fauna is so well known:

TESTUDO TEDWHITEI, new species

Type. M.C.Z. No. 2020, a complete plastron.

Type locality. Thomas Farm, Gilchrist Co., Florida.

Horizon. Arikareean Miocene.

Diagnosis. With the characters of *Testudo sellardsi* Hay (as described by Loomis 1927) but much smaller, so far as known not exceeding 400 mm. in plastral length. Pectoral scute 1/6 to 1/7 the abdominal in length of median sulcus; gulars more triangular, anals smaller; nuchal scute well developed, reaching anterior margin; costo-vertebral sulci less deeply incised; free margins less reverted.

Referred material.

M.C.Z. No. 2021, "plastron 2".
M.C.Z. No. 2022, "plastron 3".
M.C.Z. No. 2023, "plastron 4".
M.C.Z. No. 2024, "plastron 5".
M.C.Z. No. 2025, a carapace lacking some of the left peripherals,

neurals 4 and 5, part of pleural 3 and all of pleural 5 of the left side.

M.C.Z. No. 2026, a miscellaneous lot containing three anterior carapace margins, a posterior lobe of a plastron, a small femur, a humerus, a scapula and acromion, and neurals, peripherals and other carapace fragments not further identified.

Character Analysis

1. A feature of considerable interest in the new species is the size of the pectoral scute, especially its medial anteroposterior dimension. In 1950 I used a difference in this dimension to assist in distinguishing Miocene *Hesperotestudo*[1] from Miocene *Gopherus* and Miocene *Chelonoidis*, ascribing to the first a pectoral scute with "median sulcus 1/15 to 1/30 of the abdominal median sulcus", to the second a pectoral scute with "a median sulcus usually about 1/5, never less than 1/10 of the abdominal median sulcus", and to the last a pectoral scute with the "median sulcus 1/5 the abdominal median sulcus". *Testudo tedwhitei* has the following measured values for pectoral and abdominal median sulci:

Specimen	pectoral	abdominal
type	20 mm.	116 mm.
plastron 2	20	118
" 3	17	114
" 4	18	129

This range of values gives ratios of approximately 1/6 to 1/7. According to the 1950 criteria this should rank *Testudo tedwhitei* either with *Gopherus* or with *Chelonoidis*. But in major characters the new Florida form is not a *Gopherus*, and the presence of a nuchal scute excludes it from *Chelonoidis*.

If we look now at Oligocene *Hesperotestudo* we find that *T. brontops* had the pectoral median sulcus between 1/4 and 1/5 that of the abdominal, while *T. amphithorax* had the same sulcus between 1/3 and 1/4 that of the abdominal.

Testudo tedwhitei is, therefore, intermediate in this character between the Oligocene species of *Testudo* and those Miocene species of *Testudo* which previously have been well enough known to be assigned definitely to the subgenus *Hesperotestudo*. Very fortunately we are not dealing here with a single specimen in which such an aberrant or

[1] A subgenus of *Testudo* (type: *Testudo osborniana*, Miocene of Colorado) that includes all the North American members of the genus (Williams 1950). All living North American land tortoises belong to the genus *Gopherus*.

apparently aberrant character might well be an individual variation. The pectoral-abdominal ratio is clearly shown in four specimens and readily inferred in a fifth. In this regard *T. tedwhitei* seems clearly to manifest as a species character a condition more primitive than that found in *T. osborniana* and its closer relatives. *T. sellardsi* as described by Loomis (1927) is nearer in this feature to *T. osborniana* than to *T. tedwhitei*.[1]

2. In all five plastra of *T. tedwhitei* the pectoral-humeral sulcus is separated from the entoplastron by a distance equivalent to about 1/2 to 1/3 the median length of the pectoral scute itself. In *T. osborniana* and its relatives the entoplastron tends to be very close to or in contact with the pectoral-humeral boundary in spite of the extreme narrowing of the pectoral scute. In *T. brontops* and *T. amphithorax* of the Oligocene the entoplastron is also in contact with the pectoral-humeral boundary, but that is less surprising here since the pectoral scute is quite large. The difference which *T. tedwhitei* manifests in this respect from the other Miocene and the Oligocene species is not great and may probably be bridged by individual variation when more specimens are known. It does, however, seem to indicate a trend in *T. tedwhitei* different from that in *T. osborniana*, etc. With regard to this character, *T. sellardsi* and *T. tedwhitei* are quite in agreement.

3. The entoplastron cannot be accurately measured in *T. tedwhitei* except in the type and in plastron 5. In the type, the width of the entoplastron is 71 mm., its length 67 mm.; the same values in plastron 5 are 67 mm. and 59 mm. respectively. The entoplastral length is thus about 9/10 its width. In *T. osborniana* and in the closely similar forms of the Miocene and Pliocene, the length was about 3/4 the width, as it was also in the Oligocene *T. brontops*. *T. amphithorax*, on the other hand, departs in the other direction from the condition of *T. tedwhitei*, having the entoplastron slightly longer than wide (104 mm. wide, 108 mm. long, Hay 1908). According to Loomis' figure the length of the entoplastron in *T. sellardsi* must have been about 9/10 its width, as in *T. tedwhitei*.

4. Four of five plastra[2] of *T. tedwhitei* show the gular region scarcely distinct from the general contour of the anterior lobe. The same region is somewhat more developed as a projecting gular prominence in *T.*

[1] Loomis gives no measurements, but from his figure the pectoral-abdominal ratio must be between 1/12 and 1/15.

[2] In plastron 2 this area is missing.

osborniana and its group and much more developed in *T. arenivaga* of the Lower Miocene and in *T. brontops* of the Oligocene. Oligocene *T. amphithorax* and Eocene *T. uintensis*, on the other hand, have the gular prominence just as little distinct from the contour of the anterior lobe as in *T. tedwhitei*. This is equally true of *T. sellardsi*.

The striking similarity of the four plastra of *T. tedwhitei* in this as in other regards, permits much greater confidence in the use of these rather minor characters *in this group* than would otherwise be at all possible. The nearly identical differentiation of the gular region (at least in ventral view) in these four specimens is in strong contrast with the situation in *Gopherus* and in *Chelonoidis* in which individual and sexual differences in this region can be very great.

5. The dorsal aspect of the gular region, in the four specimens of *T. tedwhitei* in which this region is known, presents some interesting differences in the anteroposterior length of the swollen area and the degree of excavation of its caudal margin. The length of this "epiplastral lip" and the degree of excavation are directly correlated and, in three of the plastra, (the type and plastra 3 and 4) there is a consistent increase in both characters with size. In plastron 5, however, though it is larger than the type, both the dorsal length of the lip and the amount of posterior excavation are less, so that this region is less differentiated than in any of the other plastra. The dorsoventral thickness of the lip again varies directly as the dorsal length.

6. The inguinal scute in *T. tedwhitei* was apparently large and reached the femoral. It is satisfactorily discernible only on the left side of the type, but the partial sulci present in other specimens seem consistent with this description. A large inguinal scute is apparently characteristic of *Hesperotestudo*. A small scute is figured by Hay (1908) for *T. amphithorax*, but I have been unable to verify this on the type material at the American Museum. A small inguinal, not reaching the femoral, seems to be very characteristic of *Stylemys nebrascensis*, according to the many specimens I have examined. In Recent forms this character seems to be sufficiently constant to help in discriminating species groups; it may assist also with fossil forms.

7. The xiphiplastral notch is distinct and angular but not deep in the four plastra or partial plastra of *T. tedwhitei* in which it is preserved. In contrast, it is less distinct, wide and very shallow in *T. osborniana* and its close relatives. In both *T. brontops* and *T. amphithorax* the notch is very like that in *T. tedwhitei*. Loomis (1927)

specially commented on the distinctness of the notch in *T. sellardsi;* as he figures it, it is, indeed, very similar to that in *T. tedwhitei.*

8. With regard to the characters of the carapace we are not as fortunate as with those of the plastron, since we have only one carapace which is even approximately complete. From this, however, we may frame a rough estimate of the size and shape of the shell. The length of the carapace may be estimated as about 370 mm., the width as approximately 300 mm.; it was therefore about 4/5 as wide as long and distinctly parallel-sided, not globular. The sides were quite vertical, and the height may have been in the neighborhood of 150 mm.

In its parallel-sided contour *T. tedwhitei* was like *T. sellardsi* and rather unlike *T. osborniana* and its relatives which tend to a more nearly hemispherical carapace shape.

9. The anterolateral corners of the carapace flare above the limbs in *T. tedwhitei,* but between these flared corners, the anterior margin is essentially straight. This condition is rather characteristic of the whole assemblage which I called *Hesperotestudo* in my 1950 paper. The general impression is one of an indentation of the anterior margin, but this is not due to a real notch at the nuchal region as in some other turtles but solely to the considerable flare of the anterolateral margins.

10. The nuchal scute is preserved in three specimens in *T. tedwhitei.* In the more complete carapace it is about twice as long as wide, but in the other two instances it is significantly broader, though still longer than wide. This is another feature in which it is in general agreement with the members of the broad group *Hesperotestudo. T. sellardsi,* on the other hand, was described by Loomis (1927) on the basis of the Amherst specimen as having a very small nuchal which did not reach the anterior margin. Material referred to *T. sellardsi* at the M.C.Z. shows this scute to be of more normal *Hesperotestudo*-like character, longer than broad and reaching the anterior shell margin.

11. The vertebrals and neurals, so far as known, are essentially as in the other members of *Hesperotestudo* in which they are known. Vertebral 1 is very broad but does not reach, by a considerable interval, the second marginal of either side. Vertebral 4 is not completely known but was evidently longer than wide. Neurals 2 and 4 are octagonal (seen in two specimens). The first neural is elongate, oval in the usual fashion; neurals 3 and 5 are quadrilateral; neurals 6, 7 and 8 are hexagonal, short-sided in front.

12. The suprapygals are not distinctive; the pygal is rather narrow and bowed outward as in Loomis' figure of *Testudo sellardsi*.

13. The pleurals in *T. tedwhitei* are quite primitive in not displaying any trace of the alternate widening and narrowing of their distal ends, a feature characteristic of most advanced tortoises and seen well-developed in *T. osborniana* and *T. orthopygia*, but scarcely developed in *T. brontops* and not present in *T. amphithorax*, *T. impensa* and *T. sellardsi*.

14. The costo-vertebral sulci in *T. tedwhitei* are distinct but not deep, by no means so incised as sometimes in *T. sellardsi*. The latter, however, is a giant form, and this feature of deeply incised sulci may be suspected to be correlated with its great size. The other *Hesperotestudo* which are sufficiently known, none of quite comparable size, never show this deeply incised condition of the scute boundaries. The anterior and posterior margins are also more reverted in *T. sellardsi* than in the other forms.

15. A humerus and a small femur, both of normal testudine character, are referred to *T. tedwhitei*. The humerus has a slender rounded shaft without notable compression in any plane and with only a roughened area of attachment for the latissimus dorsi, not a pit. The femur, on the other hand, like that of *T. osborniana*, has the shaft compressed in the plane of the head and hence the shaft is rather quadrate in section.

Phyletic Relationships

The diagnosis above of *T. tedwhitei* has explicitly compared the new species with *T. sellardsi* as described from a specimen at Amherst, by Loomis (1927). I have made this special comparison because I want to evade, in the present discussion, the issue of the identity of the *Testudo sellardsi* of Loomis, described from a complete shell from Melbourne, Florida, with *Testudo sellardsi* Hay, the type of which is a xiphiplastron from Vero, Florida. Loomis' equating of his form with that of Hay may or may not be correct, but that point is not germane in the present instance.[1]

If now we compare *Testudo sellardsi*, as so defined, with *T. osborniana*, the type species of *Hesperotestudo*, certain differences are

[1] I feel it necessary to deprecate the description by anyone, even by one so experienced as Hay, of a new species of tortoise from material as poor as the type of *T. sellardsi*. Especially is it unfortunate that Hay described two species of giant tortoise from Vero from different parts of the shell!

evident. These differences, however, are not major ones. It would seem initially probable that they are merely specific and not group differences, since they are outweighed by the resemblances held in common between *T. sellardsi* and *T. osborniana*, and which separate them very clearly indeed from the species of *Gopherus*.

It therefore seemed logical, in 1950, to infer the descent of the Florida giant tortoise from *T. osborniana* or *T. osborniana*-like ancestors. But the discovery of *T. tedwhitei* changes this picture radically. It is obviously, in view of its many special resemblances, a much more suitable Miocene ancestor of the Pleistocene giant than *T. osborniana* or its close relatives. So with the entrance of *T. tedwhitei* into the picture, we see not one but two phyletic lines within *Testudo* in North America, separate at least since the Lower Miocene.

It is now desirable to set down as a first approximation the features which seem to distinguish these two phyletic lines.

Thus, the *T. tedwhitei* lineage appears to differ from the *T. osborniana* series by having:

(1) the carapace parallel-sided rather than rounded;

(2) the xiphiplastral notch distinct and angular rather than indistinct and rounded;

(3) the pectoral scute appreciably posterior to the entoplastron rather than in contact with it;

(4) the entoplastron about as wide as long rather than noticeably wider than long;

(5) the gular region less differentiated;

(6) the pectoral scute less narrowed.

None of these differences can be conceived of as an absolute difference. We are dealing not with *key* differences but with assemblages of characters that, in my judgment, empirically set apart two groups of species.

These two groups of species are indicated as closely related because of the common possession of the following characters:

1. a nuchal scute longer than wide;

2. a pectoral scute tending (with time) to become more and more narrowed;

3. an elongate fourth vertebral scute;

4. a differentiated neural sequence early acquired (in the time series);

5. markedly flared anterolateral and posterolateral margins;

6. a more convex shell than that of compared forms.

In the *T. osborniana* series in which alone skulls associated with shells are known, the characters listed above are associated with distinctive features of the premaxillary alveolar surface (a pit without a median ridge) and of the external surface of the dentary (fine vertical ribbing). These skull characters are assumed to hold for the *T. tedwhitei* series also.

In thus assuming two closely related parallel series we have two potential sources of confusion. (1) In later members of the two series, parallel variation may make closer the resemblance of forms which were distinct over a long period. Especially is this probable if, as in the present case, there appear to be similar trends with time (as in the narrowing of the pectoral scute) but trends pursued at different rates in the two series. Reversal of evolutionary trend is also a possibility. (2) The earlier members of the two series, as they approach in time their common ancestor, should be progressively less and less distinct one from the other.

Some instances of the first possibility of confusion may be expected to turn up as knowledge of Tertiary and Quaternary tortoises increases. The other point we may consider at this time in terms of the known Oligocene and Eocene tortoises.

In the Oligocene two very distinct species of *Testudo* have been described: *T. brontops* and *T. amphithorax*. On the character of the gular region, *T. brontops* with this region highly differentiated belongs with the *T. osborniana* series, and *T. amphithorax* with the same region not at all distinct, belongs with the *T. tedwhitei* series. The width-length ratio of the entoplastron arranges the two species in the same way. The pectoral scutes in both are very much wider than in Miocene forms, but in *T. brontops* the ratio of pectoral length to abdominal length is somewhat less than 1/4, in *T. amphithorax* somewhat more than 1/4, possibly an indication that the trend to greater narrowing of the pectoral was present in *T. brontops* to a somewhat greater degree than in *T. amphithorax*. This again would be consistent with a position of *T. brontops* in the *T. osborniana* line, *T. amphithorax* in the *T. tedwhitei* line. On the other hand, in certain other characters on which it is possible to distinguish the Miocene forms, no distinction is possible in the case of the Oligocene forms. In both species the pectoral-humeral sulcus is in contact with the lower margin of the entoplastron; in both the xiphiplastral notch is distinct and angular. *T.*

brontops had the carapace parallel-sided though possessing a wide shell; the shell of *T. amphithorax*, though not completely known, was probably narrower but also parallel-sided.

In the Eocene, only *T. uintensis* Gilmore has previously been referred to the genus *Testudo*. In that form the gular region is not more differentiated than in *T. amphithorax* or *T. tedwhitei*; it should therefore belong to that series. The entoplastron is about as wide as long in the unique specimen of the species; this also might count it as a member of the *T. tedwhitei* series. On the other hand, the carapace has a rounded rather than a parallel-sided contour; this might place it in the *T. osborniana* series. In still other respects it is much more primitive than any of the forms previously cited. The pectoral scute is about half the abdominal scute in length. The supracaudal scute is divided as in emydines or *Hadrianus*.

If *T. uintensis* is placed as a member of the *T. tedwhitei* series on the basis of the absence of gular differentiation, it will be to species referred to "*Hadrianus*" that we will have to look for the antecedent to the *T. brontops* — *T. osborniana* series. All so-called *Hadrianus* have a gular prominence well differentiated; this is true even of the Wasatch species. All are otherwise very primitive and differ from the forms called "*Testudo*" only in their primitiveness. Their supposed generic separation is no ground for doubting their ancestral relation to the later forms called "*Testudo*." Rather it is preferable to regard the generic distinction as invalid or at best of subgeneric value. "*Hadrianus*" *corsoni* is in most respects primitive enough to have given rise to any of the later *Testudo* of the Western Hemisphere.

In one respect only is there a difficulty and that not an important one. All the "species" called *Hadrianus* have rather parallel-sided shells combined with a differentiated gular region. *T. uintensis* has an undifferentiated gular region combined with a rather rounded shell. This is quite the reverse of the character combination we found to be present in Miocene and later species. In the Oligocene we have seen that both the assignable species have parallel-sided shells. Presumably this means only that the shell contour character, *if valid at all*, was not firmly fastened on either series until the Miocene.

This mixture and merging of the characters of the two series in the Eocene is indeed what we should expect. The series which are quite distinct in the Miocene, appear more closely approximated in the Oligocene and merge in the Eocene.

With the clearer view which the concept of two lineages within *Hesperotestudo* gives us, let us look now at certain previously problematical Miocene species. These forms poorly understood till now fall into place.

T. ducatelli Collins and Lynn (Hemingfordian Miocene of Maryland) is a form with the gular region of the plastron not distinct from the contour of the anterior lobe, the entoplastron very slightly wider than long, pectoral scute about 1/5 the abdominal in median length and touching the entoplastron on one side of the unique specimen, inguinal scute large, reaching femoral, xiphiplastral notch well-marked but not deep. The carapace except for the octagonal second neural and a few peripherals and partial pleurals is unknown. I placed this (1950, pp. 27–28), with some misgiving, as possibly a *Gopherus*, but with the new information now available I place it with much more confidence as a relative of *T. tedwhitei*.

T. farri Hay (Barstovian Miocene of Montana) is known from most of a crushed shell. The nuchal scute is longer than wide. The anterolateral corners of the carapace are not preserved. The second and fourth neurals are octagonal. The pleurals are alternately narrowed and widened distally. The gular region is not distinct from the contour of the anterior lobe. The entoplastron is just as wide as long. The pectoral scute, its anterior margin very close to but not touching the entoplastron, is about 1/7 the abdominal in median length. The xiphiplastral notch is distinct but not deep. This species, even more certainly than *T. ducatelli*, is a relative of *T. tedwhitei*.

With the addition of these forms the record of the twin lineages within *Hesperotestudo* becomes much more nearly complete, and the formerly obscured evolutionary picture is in part at least resolved into clearly defined elements. A few difficulties, however, remain:

(1) The discovery of the two lineages within *Hesperotestudo* forbids us to assign to either one of them the form *Testudo gilberti* Hay, known only from a skull. I am quite uncertain of the value of the differences described by Hay between the skulls of *T. gilberti*, *T. impensa*, *T. osborniana*, and *T. orthopygia*, and I do not think this problem will be amenable to solution until we have still more skulls *associated* with shells.

(2) There is a problem also in the allocation of *Testudo crassiscutata* Leidy of the Florida (Peace Creek) Pleistocene. In this form, unfortunately incompletely known, the anterior plastral lobe is much as in the

T. tedwhitei series, but the xiphiplastral notch is as shallow as in the *T. osborniana* series. This species may, perhaps, be provisionally placed in the *T. tedwhitei* series, but it cannot be pretended that this rather arbitrary placement implies that the situation is understood. What is the relationship of this giant form to *T. sellardsi*? What are Pliocene *T. louiseckressmani* Wark and *T. hayi* Sellards and Pleistocene *T. luciae* Hay? Were there both giant *Testudo* and giant *Gopherus* in the Florida Pleistocene? The scattered remains are tantalizing and the problems of nomenclature frustrating. Furthermore, in addition to the puzzling Florida giants there are the giant thick shelled forms of the Ashley River beds of South Carolina, in regard to which Leidy's name *Eupachemys obtusus* based on a single peripheral must be considered. This latter may possibly represent a late member of the series of which *T. tedwhitei* is now the best known example.

(3) An unfortunate nomenclatorial tangle exists. I have traced two lines of what I previously called *Hesperotestudo* back to the base of the Oligocene. If, as seems entirely probable, these two lines find their common ancestor in the earlier Eocene in some species of what has been called "*Hadrianus*", then according to modern concepts it is impossible to retain these two lineages in *Testudo*, if *Hadrianus* is accepted as a full genus. However, as I have indicated and as Gilmore had already suggested in 1915, *Hadrianus* is very imperfectly defined as against the genus *Testudo* broadly conceived. Its characters may be matched elsewhere in that genus, and it is impossible to retain the name at all unless as a subgenus. If then *Hadrianus* is regarded as a subgenus, that will obviate the major difficulty, and that solution is proposed here.

This will not, however, solve all our problems. If the apparently plausible hypothesis of the separate descent of our two lineages from forms called *Hadrianus* is true, either *Hadrianus*, as the oldest available name, must be used as the inclusive subgenus name of all North American *Testudo* (it then becomes undefinable), or alternatively a new subgenus name is required for the line of which *T. tedwhitei* is a central member. In the latter case, probably but not certainly, Leidy's name *Eupachemys* is available.

Fortunately, failure to solve this problem at this time involves no serious difficulty since all the forms concerned belong quite certainly to the genus *Testudo*.

Figure 1 presents diagrammatically the relationships as I now see them of the determinable members of North American *Testudo*.

Faunal Associations of the New Species

In addition to the excellent tortoise material which forms the hypodigm of *T. tedwhitei* there are a few additional turtle fragments which can be assigned with fair certainty to the pond turtle genus *Pseudemys* but which cannot be more precisely placed. The fragments in question (Plate 4) are one complete (unillustrated) and two partial nuchal plates, a single complete pleural, a left xiphiplastron and a left epiplastron. The delicacy of the surface sculpturing plus the greater resemblance in some minor details to individual members of the *Pseudemys floridana* group probably imply that the fragments belong to some extinct member of that group, but in the absence of more material and particularly more comparative material it is quite useless to further discuss these remains at this time.

Conspicuously absent from the preserved testudinate fauna of the Miocene of Thomas Farm are trionychids and chelydrids which are very important in the fauna of Florida today and which certainly were abundant also in the Pleistocene faunas (as considerable material at the M.C.Z. proves).

This comparative rarity of aquatic types (the absence, indeed, so far as the present record shows, of two very important aquatic turtle families) probably points as does the mammalian record (the predominance of horses, etc., Romer, 1948) to an ecology for the Miocene of Florida very different from that now characteristic of the area. "It was then, as now, a low country — but a low plain, relatively dry and grass-covered — a prairie in the western rather than the floridian sense of that term" (Romer, 1948, p. 10). The amphibian fauna recently described by Tihen (1951) would appear to point in the same direction — most abundant a species of *Bufo*, less frequent a *Rana*.

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Plate 1. *Testudo tedwhitei* new species, ventral view of type plastron. x$\frac{1}{3}$.

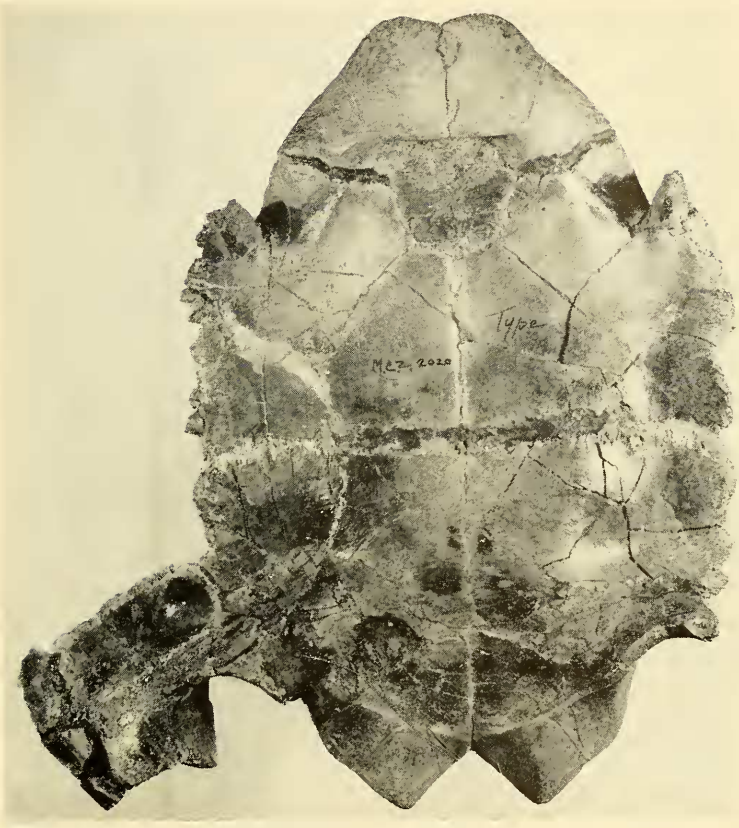

Plate 2. *Testudo tedwhitei* new species, dorsal view of type plastron. x1/3.

Plate 3. *Testudo tedwhitei* new species, referred carapace. x about $\frac{1}{3}$.

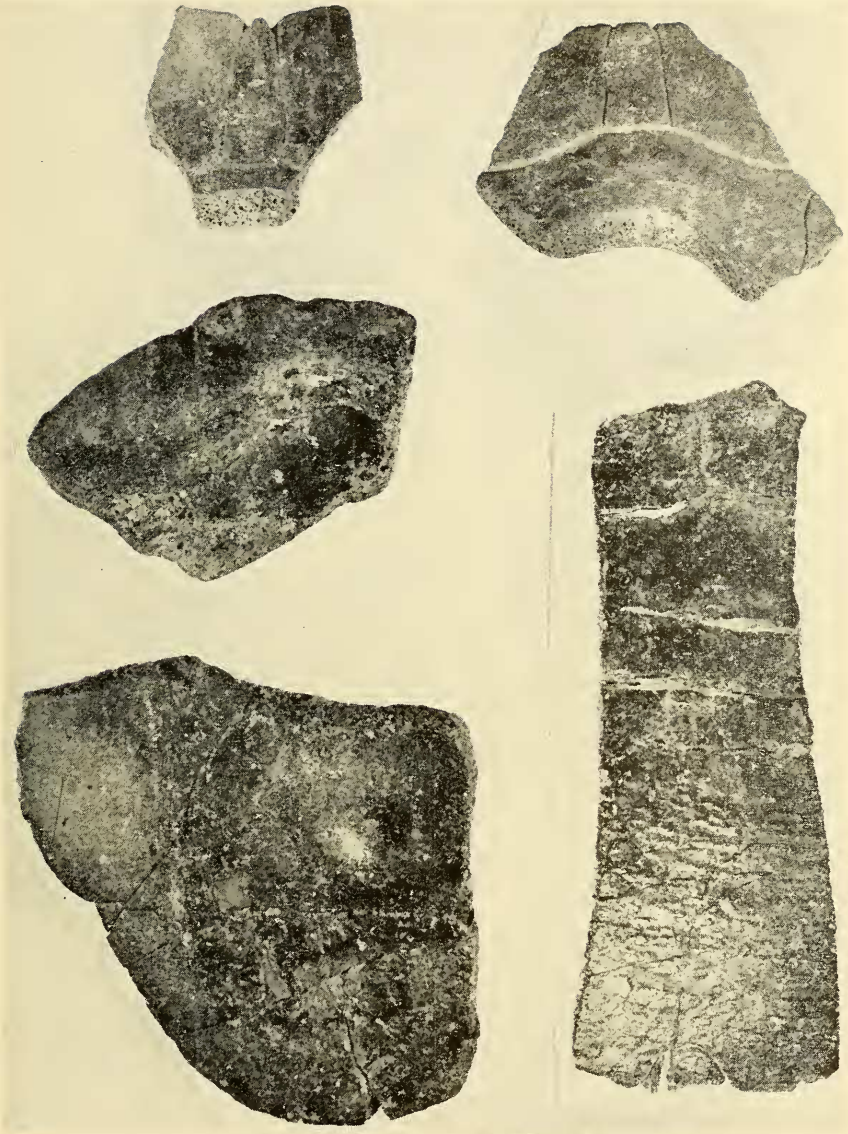

Plate 4 *Pseudemys* sp., various fragments from the Thomas Farm Miocene. x 1.

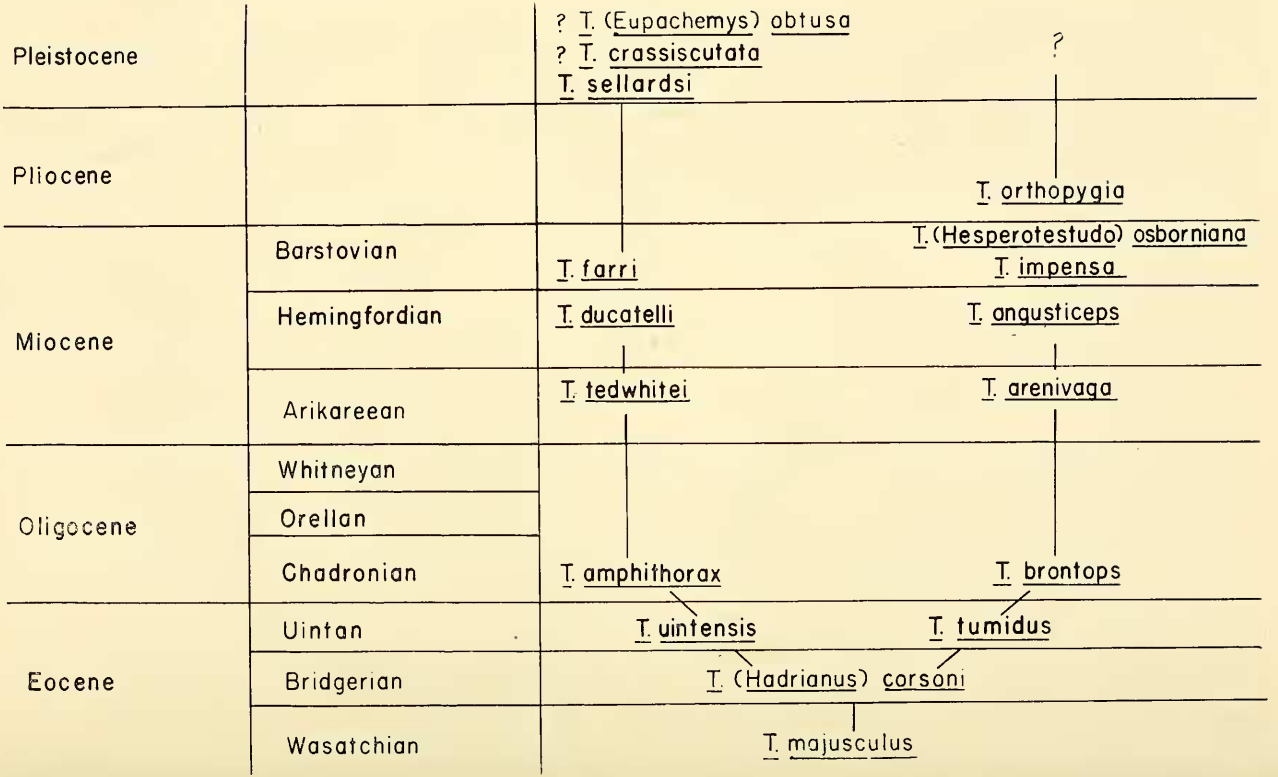

Fig. 1. Diagram of presumed phyletic relationships of North American *Testudo* species.